Best wishes,
Mel,
Obviously, your part toward this review is significant
AWS

MELODY RAY

Melody Ray-Culp

The Status of Queen Conch, *Strombus gigas*, Research in the Caribbean

ALLAN W. STONER

History of Queen Conch Research

Today there are approximately 230 published scientific papers on queen conch, *Strombus gigas*. Publication on this species began in the 1960's and increased rapidly during the 1980's and 1990's (Fig. 1). The increase in publication after 1980 was associated with three particular areas of endeavor. First, many articles were published to document the rapid depletion of conch stocks throughout the Caribbean Sea. Second, substantial progress was made in understanding processes related to growth, mortality, and reproduction in queen conch. Third, because of the apparent and widespread decline in conch, several research laboratories, especially in Florida, Puerto Rico, Venezuela, and the Turks and Caicos Islands began experiments related to hatchery production of juvenile conch. The primary intent was to replenish wild stocks by releasing hatchery-reared animals. Today, hatchery production has been relatively well perfected, and the increase in numbers of scientific papers related specifically to culture has slowed. A thorough review of the history of conch mariculture was provided by Creswell (1994), and Davis (1994) summarized the details of larval culture technique.

In the last decade significant progress has been made in our understanding of the general biology, habitat requirements, distribution, and mortality processes that influence populations of juvenile conch. There has also been considerable effort to develop techniques related specifically to stock enhancement through release of hatchery-reared juveniles. Research on stock enhancement is still increasing at a steady rate, primarily in Florida and Mexico.

Little was known about the larval biology of queen conch prior to 1980. And, while culture technique was the primary focus of larval research in the 1980's, larval ecology and fisheries oceanography are the focus of those working with conch larvae in the 1990's. The first formal descriptions of the larvae of several *Strombus* species first appeared in 1993 (Davis et al., 1993), and we can now survey larvae quantitatively in the field. Publications on larval supply and transport, nutrition and length of life of larval stages, and larval settlement and recruitment are increasing rapidly. Another area of research that is new to the 1990's is related to the role of marine fishery reserves as a management tool for queen conch. All of these issues will be discussed below.

Objectives

An important scientific workshop on queen conch was held in Caracas, Venezuela, in July 1991. This workshop and the proceedings that emerged from it (Appeldoorn and Rodriguez, 1994) provided a good background on the status

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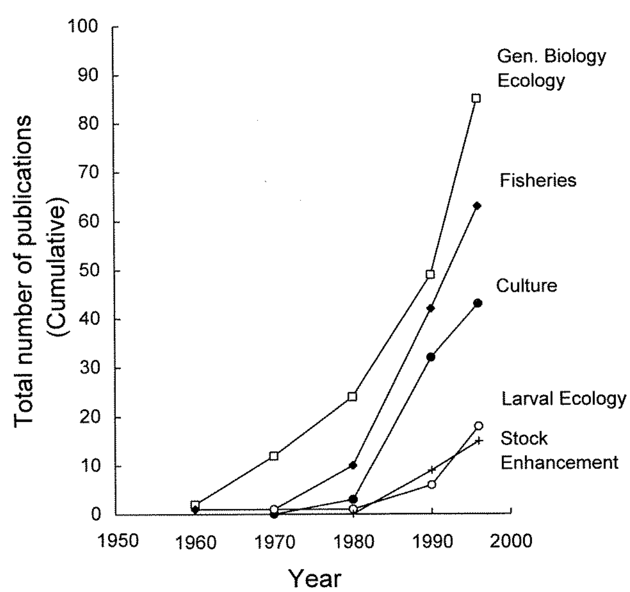

Figure 1.—Cumulative curves for the total numbers of published scientific articles on queen conch by five subdisciplines.

of research on biology, fisheries, and mariculture of the queen conch. Because the general biology of the queen conch is already relatively well known, the purpose of this paper is to summarize some of the important advances made in the study of queen conch since the 1991 workshop. Emphasis has been placed on topics related to the ecology of queen conch that are most relevant to fisheries management and stock rehabilitation. In the following sections an attempt has been made to draw conclusions about habitat requirements for the species, mortality of juveniles as it relates to stock rehabilitation and enhancement, larval ecology and fisheries oceanography of the species, and the conservation of reproductive stocks.

Habitat Requirements and Nursery Grounds

While adult queen conch are now relatively uncommon in the shallowest regions of many Caribbean banks and island shelves, the most productive nurseries for the species tend to occur in shallow (<5–6 m deep) seagrass meadows. There are, however, certain exceptions, such as in Florida, where many juveniles are associated with shallow algal flats, and on certain deep banks such as Pedro Bank, south of Jamaica. Some juveniles are found in deeper shelf locations (>10 m depth), but these constitute a large proportion of the total juvenile source only in areas where shallow-water populations are very heavily impacted by fishing or habitat destruction.

Generally, larvae are transported by surface currents from spawning grounds onto shallow banks where the larvae settle and spend their first 2–3 years of life. Long-term studies near Lee Stocking Island in the Exuma Cays, Bahamas (Stoner et al., 1994, 1996a), and in the Florida Keys (Glazer[1]) have shown that aggregations of juveniles occur in the same locations year after year. Despite expansive distribution of seagrass beds in both the Bahamas and Florida, the conch nurseries occur in very specific locations within those meadows, and vast areas of seemingly appropriate seagrass beds are never occupied by conch. Near Lee Stocking Island, 90–95% of the vast seagrass meadow appears to be unsuitable for juvenile conch. Several factors appear to be important in providing environmental conditions appropriate for juveniles in the central Bahamas, and these principles appear to be relatively universal. Most nurseries are located in areas with an intermediate density of seagrass (usually 30–80 g dry wt/m^2) and in depths of 2–4 m. On the Great Bahama Bank, the largest, most productive nurseries for queen conch are located directly in the paths of strong tidal currents, and are flushed with clear oceanic water on every tide. Recent GIS (geographic information system) models of conch distribution (Jones, 1996) show that the locations of conch nurseries can be predicted with some degree of accuracy using a combination of seagrass biomass, water depth, and tidal circulation patterns.

The association of conch aggregations with particular locations may also be related to patterns of larval settlement. Recent laboratory experiments have shown that a wide variety of biological substrata affects settlement and metamorphosis in queen conch larvae; however, substrata such as seagrass detritus and sediment taken directly from nursery grounds induce settlement at a much higher frequency than the same materials taken from non-nursery locations (Davis and Stoner, 1994). Distributional pattern in early post-settlement conch also indicates that most settlement occurs in the immediate vicinity of the long-term nursery grounds (Stoner et al.[2]). Conch larvae are known to detect and settle in response to biological cues that are associated with subsequent high growth rates in the postlarvae (Stoner et al., 1996b), and juvenile conch are known to occupy areas that have exceptionally high algal productivity. It is also possible that conch larvae are concentrated in nursery areas before settlement. This will be discussed later in the section on Larval Ecology.

The uniqueness of queen conch nursery habitats has important implications for both fisheries management and stock enhancement of this seriously overfished resource. Despite the presence of very large seagrass meadows in certain conch-producing areas such as the Bahamas, Belize, Mexico, and Florida, only relatively small sectors of the meadows may actually have production potential for queen conch, either because they lack larval recruitment features or suitability as benthic habitat. Transplant experiments indicate that most seagrass beds, in fact, cannot support juvenile conch. The most productive nursery habitats appear to be determined by complex interactions of physical oceanographic features, seagrass and algal communities, and larval recruitment. These critical habitats need to be identified, understood, and protected to insure continued queen conch population stability.

Juvenile Mortality and Stock Enhancement

For at least 20 years it has been proposed that releases of hatchery-reared queen conch could be used to enhance or rehabilitate depleted populations (Berg, 1976). Mariculture technique for conch is relatively well perfected (Davis, 1994), and there are now hatcheries in the Caribbean region, most notably the Caicos Conch Farm[3] on the island of Providenciales, capable of producing millions of juveniles each year. However, high mortality has plagued conch planting efforts since the first releases were made in the early 1980's in Venezuela, the Bahamas, and Puerto Rico (Creswell, 1994).

In recent years many investigators have examined the various factors that influence mortality rates in juvenile conch. These factors include conch size, season, abundance of predators, density

[1] Glazer, R. A. Florida Marine Research Institute, Department of Environmental Protection, South Florida Regional Laboratory, 2796 Overseas Highway, Suite 119, Marathon, FL 33050. Unpublished data are on file at the Florida Marine Research Institute.

[2] Stoner, A. W., M. Ray, and S. O'Connell. In Review. Settlement and recruitment of queen conch (*Strombus gigas*) in seagrass meadows: associations with habitat and micropredators.

[3] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

of conch, structural complexity of the habitat (e.g. biomass of seagrass), and artifacts associated with hatchery rearing. Stoner and Glazer (In Press) recently combined the results of their respective long-term experiments in the Bahamas and Florida to provide a new synthesis of mortality data for queen conch. Although increasing survivorship of juvenile conch is ordinarily assumed to be directly related to conch size and age, with some degree of refuge in size occurring between 60 and 100 mm shell length (Jory and Iversen, 1983; Ray et al., 1994), Stoner and Glazer (In Press) learned that factors such as season, year, location, and conch density can have effects on survivorship as important as size. Recently, Ray et al. (In Press) learned that there is a large suite of very small predators that consume conch in the first weeks after settlement. In Bahamian nursery grounds, the most important of these, by virtue of their abundance, were xanthid crabs less than 5 mm in carapace width.

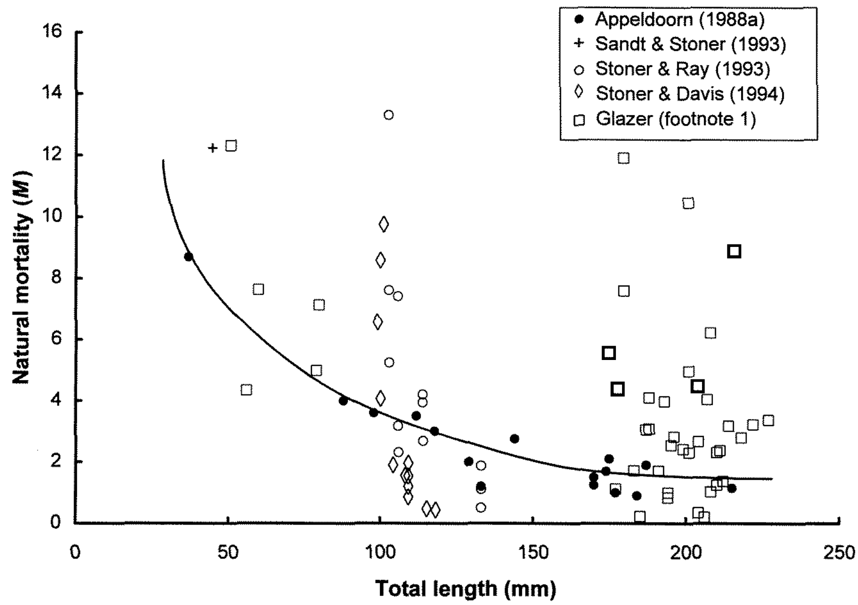

Figure 2.—Variation in instantaneous rates of natural mortality (M) for free-ranging juvenile queen conch. The curve shown was adapted from data provided by Appeldoorn (1988a) and is not intended to represent the points that are plotted for more recent investigations. Source: Stoner and Glazer (In Press).

Instantaneous rates of natural mortality (M), even in large juveniles, can vary by a factor of at least 10, from well below 1.0 to over 12.0 (Fig. 2). Because M is calculated as a logarithmic function, the probability of a conch surviving 1 year of life may vary by ten orders of magnitude, depending upon the time and location. It is clear that mortality rates of conch in natural populations can be extremely high. For example, instantaneous rates of natural mortality for small juveniles are commonly as high as 8.0–9.0. This means that an individual conch will have about a 1 in 10,000 chance of surviving over the next year.

Although hatchery production of juvenile conch is now relatively routine, hatchery-reared conch can have certain morphological, physiological, and behavioral deficiencies that increase their mortality in the field when compared with natural stocks. Stoner and Davis (1994) found that hatchery-reared queen conch grew more slowly than wild conch, had lower rates of burial, and they had shorter apical spines on the shells. All of these factors could negatively influence long-term survival of the hatchery-reared conch (Stoner, 1994). On the basis of their review, Stoner and Glazer (In Press) concluded that stock enhancement or rehabilitation that is dependent upon hatchery-reared conch has a relatively low probability of success because natural mortality rates in juvenile queen conch are high, growth rates are low, and hatchery-reared conch have numerous deficiencies. The problem is exacerbated by the continuing high cost of hatchery rearing.

It is possible that conch stocks in some locations are now so low that they cannot recover naturally. Larval recruitment data indicate that populations in U.S. waters may be in this category (see following section). In such cases, stock rehabilitation may depend on hatchery production, and the value of released conch will be determined by their survivorship to adulthood and their reproductive potential rather than their direct contribution to a fishery. Research in transgenerational enhancement may be particularly productive where populations have been severely reduced and fishing moratoria are in effect. Clearly, sound management of natural stocks is preferable to the daunting task of rehabilitating severely threatened stocks.

Larval Ecology and Fisheries Oceanography

While the culture of queen conch larvae was relatively well perfected in the late 1980's, the larvae of queen conch and closely related species were formally described only a few years ago (Davis et al., 1993). The first data on larval abundance in the field were also published in this decade (Stoner et al., 1992; Posada and Appeldoorn, 1994). Considerable progress has been made in the field of conch larval ecology and recruitment since the first descriptive studies.

We now know that conch larvae can be found in open water to depths as great as 100 m, but that most are found in the upper mixed layer of the ocean above the thermocline (Stoner and Davis, 1997b). In calm weather most are in the upper 5 m because of positive phototaxis (Barile et al., 1994). We also know that the larvae can develop in the field at rates higher than those typically observed in hatcheries using artificial diets. Davis et al. (1996) reported metamorphosis of queen conch in periods as short as 14 days for larvae reared in field enclosures with natural assemblages of phytoplankton for food. Growth rates are strongly temperature dependent and sensitive to the amount and types of phytoplankton food available in the water column (Davis[4]). However, we have also learned that the larvae are capable of remaining in the water column for very long periods of time (perhaps 2 months) after reaching metamorphic competence (Noyes, 1996), and queen conch larvae have been collected in the mid-Atlantic Ocean near the Azores (Scheltema[5]).

The supply of conch larvae has a very important role in determining recruitment of conch to the nursery grounds and to the fishery. Recently, it has been shown that there is a direct positive relationship between the mean densities of late-stage larvae and the sizes of the juvenile populations in nursery grounds in both the Florida Keys and in the Exuma Cays, Bahamas (Stoner et al., 1996c). While the exact relationship was different in the two geographic regions, the fact that there is a close correlation between larval supply and juvenile population size within the systems indicates that the nursery grounds are not saturated with juveniles (i.e. the nurseries are below carrying capacity). Also, a positive correlation between year-class strength and larval supply has been observed near Lee Stocking Island in the Bahamas (Stoner[6]). These correlations, over both spatial and temporal scales, suggest that the populations of juvenile conch may be recruitment limited and that larval supply may determine the strength of recruitment on at least the local scale.

We have also observed that the locations of conch nurseries may be determined in part by local patterns of abundance in conch larvae. Near Lee Stocking Island, highest densities of late-stage queen conch larvae were found directly over locations known to support large aggregations of juvenile conch during surveys spanning seven years (Stoner and Davis, 1997a). Large, stable aggregations of juvenile queen conch were consistently supplied with high densities of larvae and were directly associated with tidal channels carrying larvae from offshore spawning grounds. In contrast, more ephemeral aggregations were characterized by low or inconsistent veliger densities (particularly late-stage larvae), and were generally outside primary tidal current pathways. Distribution of juvenile queen conch appears to be directly related to the horizontal supply of larvae.

Correlations between larval supply and juvenile population size over both spatial and temporal scales, along with data from transplant experiments, suggest that populations of queen conch are often recruitment limited, not habitat limited. Larval limitation implies that pre-settlement phenomena, such as growth and mortality during planktonic stages and larval transport, may be critical to population dynamics in queen conch. The positive relationship between larval supply and population size suggests that we need to understand transport processes and the mechanisms affecting larval supply to nursery grounds in order to understand recruitment process and year-class strength.

The relationship between oceanography and delivery of queen conch larvae to nursery grounds has been investigated in two systems: in Exuma Sound, Bahamas, and in the Florida Keys. Both studies show the dependence of populations upon upstream spawners.

In Exuma Sound, prevailing summer surface currents carry larvae away from the eastern rim of the Sound near Cat Island and onto the banks near the Exuma Cays on the western side of the Sound. Also, mesoscale gyres in Exuma Sound generally advance toward the northwest (Hickey[7]), transporting and concentrating larvae in the northern end of the system. The result is very large juvenile populations in the northern Exuma Cays and southern Eleuthera, and an historic record of high fisheries productivity in the northern Sound (Stoner, In Press). The full oceanographic interpretation of this mesoscale phenomenon is in progress.

The delivery of larvae to nursery grounds in the Florida Keys has also been analyzed (Stoner et al., 1997). In Florida, the queen conch population was reduced to such an extent that all conch fishing was banned in 1985. Between 1992 and 1994, estimates for the total number of adult queen conch in the entire Florida Keys island chain (250 km long) were between 5,800 and 9,200 individuals, and the Florida Department of Environmental Protection concluded that the population had shown no sign of recovery (Glazer and Berg, 1994; Glazer[8]). The fishing moratorium is still in effect.

Because there were so few queen conch in the local reproductive stock, Stoner et al. (1996c) postulated that the population in Florida is replenished with larvae produced outside the United States in the western Caribbean Sea (Mexico and Belize) and delivered to the nurseries on the Florida Current. To test this hypothesis, 35 collections of larvae were made in the Looe Key National Marine Sanctuary during the reproductive seasons of 1992 and 1994, concurrent with the deployment of a current meter array immediately offshore. In brief, most of the queen conch larvae collected at Looe Cay were late-stages that arrived in association with northward meanders of the Florida Current (Stoner et al., 1997). Late-stage conch larvae were never collected when the north wall of the Florida Current was offshore in the Florida Straits.

There are large spawning stocks in Belize and Mexico and recruitment of late-stage queen conch during periods of high eastward flow at Looe Key is consistent with the hypothesis that they have a source in the western Caribbean

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[4] Davis, M. (In prep.). The effects of natural phytoplankton assemblages, temperature, and salinity on the length of larval life for a tropical invertebrate. Ph.D. dissert., Fla. Inst. Technol., Melbourne.

[5] Scheltema, R. S. 1995. Woods Hole Oceanographic Institution, Woods Hole, MA 02543. Personal commun.

[6] Stoner, A. W. Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 74 Magruder Rd., Highlands, NJ 07732. Unpublished data are on file in the author's laboratory.

[7] Hickey, B. A. 1996. School of Oceanography, University of Washington, Seattle, WA 98195. Personal commun.

[8] Glazer, R. A., K. J. McCarthy, R. L. Jones, and L. Anderson. (In review). The use of underwater metal detectors to locate outplants of the mobile marine gastropod, *Strombus gigas* L.

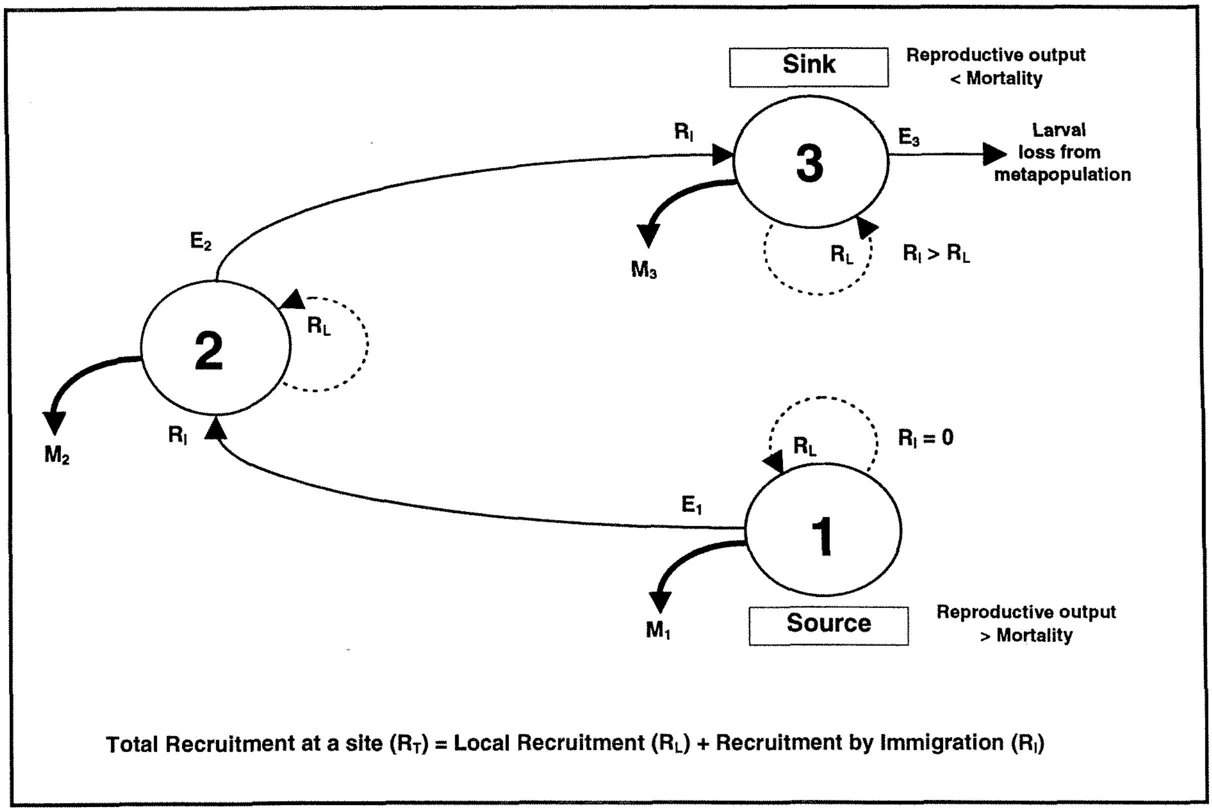

Figure 3.—Conceptual model of metapopulation dynamics. The model assumes a general circulation of water carrying larvae from Population 1 to 2 to 3. See text for definition of the model parameters.

Sea. The 3- to 4-week development period for queen conch larvae (Davis et al., 1993) in combination with average current velocities in the Loop Current and Florida Current system would permit transport from the Yucatan Strait to the Florida Keys. Concentrations of late-stage larvae are known to be high in the Florida Current 35 km south of the middle Keys (Stoner et al., 1996c), and arrival of conch larvae in association with easterly flow at Looe Key suggests that larvae of Caribbean origin are being delivered by the Florida Current. Although the genetic similarity between queen conch in the Caribbean Sea and Florida indicates significant gene flow (Mitton et al., 1989; Campton et al., 1992), the recent study by Stoner et al. (1997) provides the first oceanographic data indicating that a population of queen conch is dependent upon a source in an upstream nation.

It is possible that queen conch populations in Florida were historically self-sustaining, when adult populations were large. Today, however, recruitment appears to depend to a large extent on irregular and unpredictable northward meanders of the Florida Current. This would explain the lack of recovery in spawning stocks of queen conch since the fishing moratorium was established in 1985. Rehabilitation of this stock may now depend upon transplanting spawners or releasing hatchery-reared juveniles. However, stock enhancement through release of juveniles is difficult and expensive because of high potential mortality (described earlier) and has a history of low success (Stoner, 1994; Stoner and Glazer, In Press). Wise management and transgenerational enhancement of marine fishery resources will depend upon extensive knowledge of larval transport and recruitment processes.

Sources of larvae may be local if retention mechanisms are strong, or they may be distant, supplied by other nations. Although little is known about large-scale patterns of abundance and larval transport for any species in the Caribbean region, it is likely that most of the national populations are interdependent because of larval drift. This "open" nature of the populations requires that population dynamics be considered from a metapopulation perspective (Gilpin and Hanski, 1991). In the theoretical model presented in Figure 3 there are three subpopulations connected by larval transport. Population 1 is maintained by local recruitment (R_L) and has no recruitment by immigration from other sources (R_I). Reproductive (larval) output from Population 1 is greater than local mortality (M), and some of that output is exported to downstream populations (E). In metapopulation terminology, this population is a "source." Populations 2 and 3 are downstream from Population 1 and receive larvae both from local spawners (R_L) and from upstream sources (R_I). By definition, Population 3 is a "sink" because reproductive output is less than local mortality, and most larval production is lost from the system. Population 2 is a "source" for Population 3, but may also be a "sink" depending upon the relationship between R_L and M_2.

Practical examples of "sources" and "sinks" can be hypothesized in the Caribbean region. The Windward Islands are probably "source" locations, analogous to Population 1 in the model because of the general east-to-west circulation of surface waters through the Caribbean Sea. In the eastern Caribbean, populations of queen conch and other species with pelagic larvae must be maintained by local recirculation patterns. Island-scale self-recruitment mechanisms have been discussed in general by Farmer and Berg (1989), and more specifically for Bermuda (Schultz and Cowan, 1994) and Barbados (Cowan and Castro, 1994), which are probably dependent upon local retention of fish larvae. Florida conch populations may receive larvae from local spawning populations; however, the populations are so low today that Florida is probably a "sink" with heavy dependence upon upstream sources of larvae, as described earlier. Important conch-producing locations such as Belize and Pedro Bank are probably more analogous to Population 2 in the model, with characteristics of both "sources" and "sinks."

Position within the metapopulation structure can have important management consequences. For example, a source population will be highly vulnerable to recruitment overfishing, and emphasis must be placed on maintaining an effective and sustainable reproductive stock quality. Downstream populations are also dependent upon larvae from these source populations. A sink-type population is more susceptible to management practices occurring in the upstream source locations than to those effected by local management practice. Recovery of depleted stocks requires an adequate source of larvae which may or may not be local. For these reasons, a strong effort should be made to identify the sources of larval recruitment for target populations, and stock management should be based upon the associated metapopulation structure.

Conserving Reproductive Stocks

It is obvious from the previous discussion that it is important to maintain a regular, high-density supply of larvae to queen conch nurseries by preserving reproductive populations of adequate size. Reproductive stocks and reproduction are protected by a variety of management techniques that have been discussed by others. In this section, results from two new investigations bearing on the role of conch reproduction are described.

In the summer 1995, the Caribbean Marine Research Center conducted surveys of adult conch in the Exuma Cays, Bahamas, to test for hypothesized relationships between adult conch density and reproductive behavior (Stoner[9]). Protection of conch in the Exuma Cays Land and Sea Park presented the unusual opportunity to examine a wide range of spawner densities, from a few conch per hectare to approximately 650 per hectare. The surveys showed that 10–30% of the conch were usually laying eggs at any one time and place during the summer reproductive season, but the data suggest a decline at densities less than about 50 adult conch/ha. Similar declines were observed in the relative abundance of mating pairs of conch at about 50 conch/ha. Given that reproduction in queen conch requires internal fertilization of eggs, it is possible that some threshold of adult density is required for males and females to detect one another and mate. The exact density at which reproduction is depressed probably varies with location, the overall size and scale of the population, and natural aggregation of adults during the summer spawning season. However, it is clear that a minimum spawner density is important for successful reproduction in queen conch (Appeldoorn, 1988b). While quantitative surveys have been made in relatively few locations in the greater Caribbean region, 50 adult conch/ha is significantly higher than the densities reported in many locations, including Bermuda, Florida, Puerto Rico, the U.S. Virgin Islands, and Venezuela, in recent years (Stoner and Ray, 1996).

There are at least two ways to protect high densities of adult queen conch: depth refugia and marine reserves.

Depth Refugia

Queen conch are herbivorous, consuming micro- and macroalgae throughout their lives as benthic juveniles and adults. Therefore, conch are found in well-lighted regions of the marine environment from the shallowest subtidal zone down to depths of about 35–40 m in clear Caribbean water. There have been a few reports of queen conch observed in depths to 60 m but these individuals are very rare.

Detailed depth distributions for adult conch have been reported for Puerto Rico, the U.S. Virgin Islands, and the central Bahamas. In Puerto Rico, maximum adult density occurred at 20–25 m, but the densities at this depth were very low (0.05 conch/ha) (Torres Rosado, 1987). This deep distribution of adults was attributed to fishing pressure. In less heavily fished waters of the U.S. Virgin Islands, maximum adult density was (17.1 adults/ha) in a depth range of 18–24 m (Friedlander et al., 1994). Near Lee Stocking Island in the Bahamas, maximum density (88 adults/ha) was observed in 15–20 m depth, and densities were approximately 18 adults/ha in 20–25 m depth (Stoner and Schwarte, 1994), similar to values in the Virgin Islands. Although direct comparisons must be made with caution, it is clear that where fishing is open to scuba diving, as in Puerto Rico, maximum abundance of adult conch is driven to great depth, and numbers at all depths are generally very low. This is in sharp contrast with relatively natural populations of adults in the Exuma Park where the highest abundance of adults (270 adults/ha) occurs in depths

[9] Stoner, A. W. Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 74 Magruder Rd., Highlands, NJ 07732. Unpublished data are on file in the author's laboratory.

of just 10–15 m (Stoner and Ray, 1996; Table 1). In the Bahamas, where fishing is limited to free diving, adult conch are relatively uncommon in depths shallower than 10 m but densities increase rapidly with depth beyond the reach of the average free-diving conch fisherman.

Very few conch live deeper than 30 m, and virtually all are accessible to scuba divers. One potential form of management for a healthy reproductive population, therefore, is to limit fishing to free diving. However, because the vast majority of queen conch spend their first 2–3 years in shallow water, young adults and adults that do not migrate to deep water are all accessible to free divers, it is possible that intense fishing for conch in shallow water could ultimately reduce deep-water stocks. This apparent dilemma was discussed earlier by Stoner and Ray (1996).

Marine Reserves

Closed areas represent another mechanism for maintaining high densities of adult conch. The Exuma Cays Land and Sea Park is a marine fishery reserve established in 1958 and administered by the Bahamas National Trust in the central Bahamas. The Park is large, spanning a section of the northern Exuma Cays 40 km long and 8 km wide. No fishing of any kind has been permitted since approximately 1984. Stoner and Ray (1996) conducted extensive, depth-stratified surveys in the Park and near Lee Stocking Island to compare the abundance of adults, juveniles, and larvae of queen conch in a marine fishery reserve and in a nearby fished area of the Exuma Cays. Large differences in densities of adult conch between the reserve and the fished area are obvious (Table 1). Differences in densities of adult conch were significant in all depth zones down to 30 m, except in the very shallow shelf region (0–2.5 m depth), and, as would be expected, this marine reserve conserves spawners. One of the most notable differences between the two sites was that densities were 30 times higher in the shallow bank environment of the reserve than in comparable habitat in the fished area. The bank represents a very large habitat in the Exuma Cays and the contribution of the bank to the adult population was enormous. Additionally, conch density on the bank in the reserve was sufficiently high to promote reproduction in that habitat.

Table 1.—Density of adult queen conch in the Exuma Cays Land and Sea Park near the island of Waderick Wells and in the fished area near Lee Stocking Island, Exuma Cays. Values for adult density are mean ± SE for each depth interval. The bank habitat was represented by a 5 km wide band of the shallow (0–5 m deep) Great Bahama Bank immediately to the west of the island chain. The shelf habitats were to the east of the islands where depths increased gradually out to the shelf-break which began at about 30 m depth. Stoner and Ray (1996) provide full details.

Habitat/ depth (m)	Marine reserve	Fished area
Bank	53.6	1.7
Shelf		
0.0–2.5	0 ± 0	0 ± 0
2.5–5	34 ± 22	2.2 ± 1.7
5–10	49 ± 18	7.2 ± 4.1
10–15	270 ± 85	60 ± 47
15–20	104 ± 58	88 ± 32
20–25	148 ± 72	18 ± 9
25–30	122 ± 70	0 ± 0

Because of the high abundance of spawners, there were about 10 times more newly-hatched larvae in the unfished area than the fished area (Stoner and Ray, 1996). An alongshore drift of about 1.5–3 km per day and a mesoscale gyre in the northern Exuma Sound then carry larvae produced in the fishery reserve to nurseries in the northern Exuma Cays and southern Eleuthera. Reports from fishermen and from the Department of Fisheries indicate that the numbers of juvenile conch have increased in these areas over the last 10 years, the time period during which fishing has been closed in the Exuma Park. Although the observations must be considered anecdotal, the high production of larvae in the fishery reserve undoubtedly contributes to fished populations in downstream areas.

The apparent success of the Exuma Cays Land and Sea Park in protecting spawning stocks of queen conch and in producing high numbers of larvae for export to surrounding areas is due, in part, to its large size (about 320 km^2). Reserves must be large enough such that most of the reproductive stock cannot migrate out of protected areas to be captured. We also need to consider larval transport and physical oceanography in the design of fishery reserves. They must receive a regular supply of larvae from some spawning population, and they must be established in locations that will contribute to the downstream fishery. Reserve design should be developed in the context of metapopulation dynamics discussed earlier.

Conclusions

Research on queen conch continues to accelerate because of stock depletion throughout the Caribbean region and interest in stock rehabilitation. Recent advances are related to habitat requirements and survivorship of juveniles, larval ecology, fisheries oceanography, and certain management practices.

The majority of juvenile conch occur in a few unique habitats. These nursery grounds are defined by a suite of abiotic and biotic characteristics, including water circulation, patterns of larval accumulation and settlement, production of foods, and differential mortality. These nursery habitats must be identified and protected from destruction.

Stock enhancement through release of hatchery-reared conch has not been successful because of low growth rates and high natural mortality in juvenile conch. Release techniques are improving in parallel with good information on the variables that affect the highly variable mortality rates, but seed costs remain high, and hatchery-reared conch bear certain physiological, morphological, and behavioral deficiencies.

Recruitment to the juvenile class appears to be dependent upon the numbers of larvae supplied to the nursery grounds, on both spatial and temporal (interannual) scales. Locations with large populations of juveniles and adults receive regular deliveries of conch larvae in high density.

Populations of queen conch within the Caribbean region are probably interdependent because of larval drift on ocean currents for periods of time between two weeks and two months. The extent of interdependence among populations and among nations is poorly known; however, management of the conch resource must be considered within a metapopulation context. The significance of larval drift to fisheries management is an area of research that warrants much new research.

Successful reproduction of queen conch is related to adult density, particularly at low density. Although the lower threshold for normal reproductive behavior is unknown, density-dependent reproductive behavior has important management implications and should be explored.

Populations of queen conch significant to the fishery all occur within the depth range of scuba divers, consequently all conch are vulnerable to this form of fishing pressure. Given that relatively healthy populations of conch are now limited primarily to nations where scuba is prohibited in the collection of conch, this form of management appears to have a positive effect.

Marine reserves can protect adult populations of queen conch and supply larvae to fished areas downstream from the reserves. Fishery reserves protect the integrity of spawner density for high reproductive efficiency and larval production. The size of reserves needs to be large enough to prevent the adult stocks from emigrating readily over the reserve boundaries, and the location should be chosen with the objective of producing larvae that will be carried to suitable downstream nursery areas.

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